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# Importance of alternative foods on the persistence of flavor aversions: implications for applied flavor avoidance learning

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**Abstract**

We added a novel flavor, citric acid (CA), to a familiar test diet and conditioned an aversion in lambs to the flavored diet using lithium chloride. In 1 h feeding trials, we examined the roles of a novel flavor cue, choice and nutritional quality of alternatives on the persistence of an aversion. Availability of alternative foods increased the persistence of the aversion to the CA-flavored test diet. Furthermore, persistence was related to the energy content of the alternative. The higher energy alternative better complimented the high protein content of the basal ration (alfalfa pellets) and increased persistence versus the lower energy alternative. Continued avoidance of the CA-flavored test diet was observed even after a 68-day intermission among lambs with access to alternatives. We submit that application of flavor avoidance learning (FAL) may be useful for minimizing herbivory when a novel flavor is employed and alternative forage is present. Published by Elsevier Science B.V.

*Keywords:* Alternatives; Flavor avoidance learning; Herbivory; Persistence

## 1. Introduction

Many plants have evolved defensive systems that employ toxins and chemical cues (Bryant et al., 1991). These toxins can produce negative post-ingestive consequences in herbivores, effectively defending the plants from mammalian herbivory via aversive conditioning (Provenza, 1995). Furthermore, the phytochemical cues associated with the aversion need not be toxic themselves. Recognition of this mechanism, often termed

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flavor avoidance learning (FAL), suggests that detrimental herbivory to agricultural resources may be minimized by employing a similar strategy.

A wide variety of wildlife damage agricultural resources or become threats to human safety. Annually, wildlife are thought to cause US$ 0.6–1.6 billion worth of damage to agricultural resources in the US (Wywialowski, 1998). Scientifically sound, safe, effective, economical and socially acceptable methods are needed to alleviate undesirable wildlife–human interactions. Applied FAL offers the promise to reduce damage to agricultural resources by herbivores while also meeting these goals.

Numerous studies of FAL have been conducted that suggest FAL may be useful in wildlife damage management applications (Reidinger and Mason, 1983; Reidinger, 1997). In reality, application of FAL has enjoyed few successes in wildlife damage management. Aversive conditioning of predators to minimize livestock depredation showed initial promise, but today is considered a failure (Conover and Kessler, 1994). In some management practices, FAL can actually prove detrimental to management objectives (El Hani et al., 1998). Conversely, one of the few acknowledged successes of applied FAL in wildlife damage management has been the use of the carbamate pesticide (methiocarb) for reducing frugivory (Dolbeer et al., 1994).

We contend that successful transfer of FAL from the laboratory to the field may hinge upon four critical factors: (1) salience of the cue; (2) dose and pharmacology of the toxin (unconditional stimulus; UCS); (3) availability of alternative foods; (4) social facilitation. Novelty is extremely important to the salience of the cue (Provenza et al., 1995). In fact, it is very difficult to form an aversion to familiar foods because the animals have already learned that the flavor has no toxin associated with it (Provenza et al., 1996). Many studies have already outlined the important elements of the UCS. The avoidance response is highly dependant on UCS concentration (Launchbaugh and Provenza, 1994; Kyriazakis et al., 1998) and toxic effects (Conover, 1989; Kyriazakis et al., 1997; Gill et al., 2000). Once averted, animals must have foraging options. For instance, livestock will ingest toxic plants they typically avoid when no other forage is available (Provenza et al., 1992). Finally, social interaction with conspecifics plays a major role in maintaining or extinguishing learned aversions (Galef, 1985; Ralphs and Provenza, 1999).

This study addresses two of these factors: the importance of the cue and forage alternatives. We used lambs as model herbivores and designed a study to: (1) change the flavor of a familiar, highly desirable test diet by the addition of citric acid (CA); (2) condition an aversion to CA-flavored diet; (3) offer the CA-flavored diet and alternative foods varying in nutritional quality to averted subjects. We measured intake of the test diet to determine the importance of novel flavor and food alternatives in achieving the desired effect, i.e. reduced intake of a desirable resource.

## 2. Methods

### 2.1. Subjects

Thirty-two lambs (3-month old commercial cross-breds) were maintained as a flock at the Utah State University Green Canyon Ecology Center in Logan, UT for use in the main experiment. The flock was provided ad libitum access to the food components used in the bioassays (corn, barley, beet pulp, grape pomace and alfalfa) for 7 days. After being placed in individual pens (9 $m^2$), lambs were provided ad libitum access to water and mineral block. Sixteen additional lambs were used in a bioassay designed to determine the effects of CA on food intake. These individually penned lambs were not familiarized to the food components.

Bioassays commenced daily at 8:30 h and were immediately followed by unlimited access to a basal ration of alfalfa pellets until 18:00 h, when pellets were removed. This deprivation schedule was employed throughout the study. Study foods were presented in 13 $cm^3$ plastic food containers. This study was conducted according to procedures approved by the Utah State University Institutional Animal Care and Use Committee.

### 2.2. *Study foods*

The ground test diet consisted of beet pulp (a source of slowly fermentable energy), corn (a source of highly fermentable energy) and soy bean meal (a source of protein, Table 1). Grape pomace was added to provide a distinctive flavor. Barley was combined with alfalfa in varying proportions to yield two foods (high energy alternative (HEA) and low energy alternative (LEA)) that differed in nutritional content (Table 1; NRC, 1985). Test diet was highest in energy among the study foods. The basal ration (alfalfa pellets) was higher in protein content than any of the three study foods (Table 1).

### 2.3. *CA effect*

A bioassay was conducted to determine if CA reduced intake in the absence of an aversion induced by lithium chloride. Sixteen lambs, unfamiliar with the test diet, were assigned to either the control or treatment group such that mean basal intake was similar between them. Control subjects were offered test diet only, while treatment subjects were offered test diet with 1% CA. The 1 h no choice tests were conducted for five consecutive days. During the bioassay, lambs were subjected to the deprivation schedule as previously described.

### 2.4. *Pre-exposure feeding trials*

The main experiment began with pre-exposure feeding trials conducted on 4 consecutive days with 32 lambs. These trials were conducted to measure preferences among the foods

Table 1
Foods used in the bioassay studies[a]

| Food | Energy (kJ/g) | Protein (%) | Constituents |
|---|---|---|---|
| Basal ration | 10.3 | 17.0 | Alfalfa (pellets) |
| Test diet | 13.5 | 13.5 | 40% Corn; 10% soybean meal; 35% sugar beet pulp; 15% grape pomace |
| LEA | 11.4 | 16.3 | 20% Barley; 80% alfalfa |
| HEA | 13.0 | 15.3 | 50% Barley; 50% alfalfa |

[a] All constituents were ground unless otherwise noted. Calculated nutritive content for the mixtures based on NRC (1985) values for the individual constituents and their proportions.

Table 2
Bioassay design for the main experiment[a]

| Experiment day | Component | Treatment | | | |
|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 |
| 0 | Exposure | Test diet | Test diet (CA) | Test diet (CA) | Test diet (CA) |
| 0 | Aversion | LiCl | LiCl | LiCl | LiCl |
| 1–12, 81, 82, 83 | Persistence | No choice: test diet | No choice: test diet (CA) | Two-choice: test diet (CA); LEA | Two-choice: test diet (CA); HEA |

[a] Presence of 1% citric acid in test diet indicated by (CA). Test diet, LEA, and HEA constituents provided in Table 1.

tested, ensure that the test diet was familiar and to assign subjects to treatment groups. The first test was a two-choice test conducted with 500 g each of the test diet and the LEA (Table 1). Choices were offered in 1 h tests and intakes were recorded. The following day, subjects were similarly offered 500 g each of the test diet and the HEA (Table 1). Because a few lambs nearly exhausted the test diet midway through the trial, this choice test was terminated at 30 min, so preference would not be impacted by differences in availability.

To help ensure familiarity with the test diet, all 32 lambs were offered 600 g of test diet for 1 h on the third day of pre-exposure trials. Subjects were allowed to exhaust their supply of the food. On the last day of pre-exposure trials, lambs were offered 800 g of test diet for 1 h and intake was recorded. No subjects exhausted the test diet. These intake data were used for assigning the 32 subjects to four treatments.

### 2.5. *Exposure*

Subjects were assigned to one of four treatments (eight lambs each) such that pre-exposure test diet intake (last day of pre-exposure trials) was balanced among treatments. On day 0, lambs were offered 800 g of test diet or test diet plus 1% CA for 1 h according to treatment design (Table 2). Intake was recorded. Upon completion of the exposure trial, subjects immediately received lithium chloride (200 mg LiCl/kg body mass) by oral gavage. Because the aversion-inducing effects of lithium chloride occur during the first hour following administration, alfalfa pellets were withheld for 2 h following LiCl delivery to ensure a strong aversion to the test diet and not to the alfalfa pellets (Provenza et al., 1993). Following exposure, one subject (a member of treatment 3) was diagnosed with coccidiosis and removed from the experiment.

### 2.6. *Persistence*

Lambs were offered foods according to treatment design (Table 2). Eight hundred grams of each food were offered in no- and two-choice tests for 1 h each morning for 12 days. Intakes of test diet and alternatives (LEA or HEA) were recorded. Following a 9-week intermission, the bioassay was resumed for 3 days (Table 2). Two subjects (one each from treatments 2 and 3) were not available for resumption of the bioassay on days 81, 82 and 83.

### 2.7. Statistical analyses

The effect of CA in the absence of an aversion was tested by repeated measures analysis with intake the response. Treatment, day and treatment × day were the fixed effects and subject (nested in treatment) the random effect (SAS mixed procedure; Littell et al., 1996).

Data from the two pre-exposure preference tests were tested separately. Intake ratios (test diet/alternative) were calculated for each subject and compared to the value of no preference (ratio = 1) with $t$-tests of the means.

Lamb response to lithium exposure was assessed with a two-factor ANOVA of days 0 and 1 data. Treatment, day and the interaction were fixed effects and subjects nested in treatment was the random effect. Test diet intake was the response. Persistence data (days 1–12, 81, 82 and 83) were similarly analyzed as a repeated measures analysis with treatment, day and treatment × day the fixed effects and subjects (treatment) the random effect. Linear contrasts were used to answer the a priori questions, does CA reduce test diet intake in the presence of an aversion $[l_1 = \mu_1 - 1/3(\mu_2 + \mu_3 + \mu_4)]$; and does access to alternatives reduce test diet intake more than addition of CA alone $(l_2 = \mu_2 - 1/2[\mu_3 + \mu_4])$.

Extinction of the aversion was measured by plotting persistence and pre-exposure intake data with 95% confidence intervals. Extinction was defined as the first time period that the test diet intake confidence interval intersected the pre-exposure intake confidence interval.

## 3. Results

In the absence of lithium toxicosis, CA reduced test diet intake ($F_{1,14} = 5.31$; $P = 0.037$). Mean intake of the control subjects was 745 g (S.E. = 32), while treatment intake was 597 g (S.E. = 28). Intake increased over days ($F_{4,55} = 13.05$; $P < 0.0001$), but treatment and day did not interact ($F_{4,55} = 0.29$; $P = 0.88$).

Lambs preferred the test diet to either alternative in pre-exposure trials. Test diet was preferred 8.7–1 over LEA ($t = 3.66$; $P < 0.0004$) and 2.5–1 over HEA ($t = 4.07$; $P < 0.0002$). Following exposure, test diet intake was reduced on day 1 by LiCl administration in all treatments as evidenced by a significant day effect ($F_{1,27} = 186.4$; $P < 0.0001$) and the absence of a day × treatment interaction ($F_{3,27} = 1.12$; $P = 0.36$; Fig. 1). No visible signs of illness were observed following the single LiCl exposure and all subjects consumed the basal ration when offered at 2 h post-exposure.

Repeated measures analysis of intake post-exposure (persistence) indicated that test diet intake was influenced by treatment ($F_{3,28} = 22.81$; $P < 0.0001$), day ($F_{14,374} = 45.99$; $P < 0.0001$) and the interaction of day and treatment ($F_{42,374} = 3.00$; $P < 0.0001$). Furthermore, linear contrasts indicated that the addition of CA to the test diet reduced intake in the presence of an aversion ($l_1$: $F_{1,28} = 46.13$; $P < 0.0001$) and access to alternatives reduced intake more than addition of CA alone ($l_2$: $F_{1,28} = 18.99$; $P = 0.0002$).

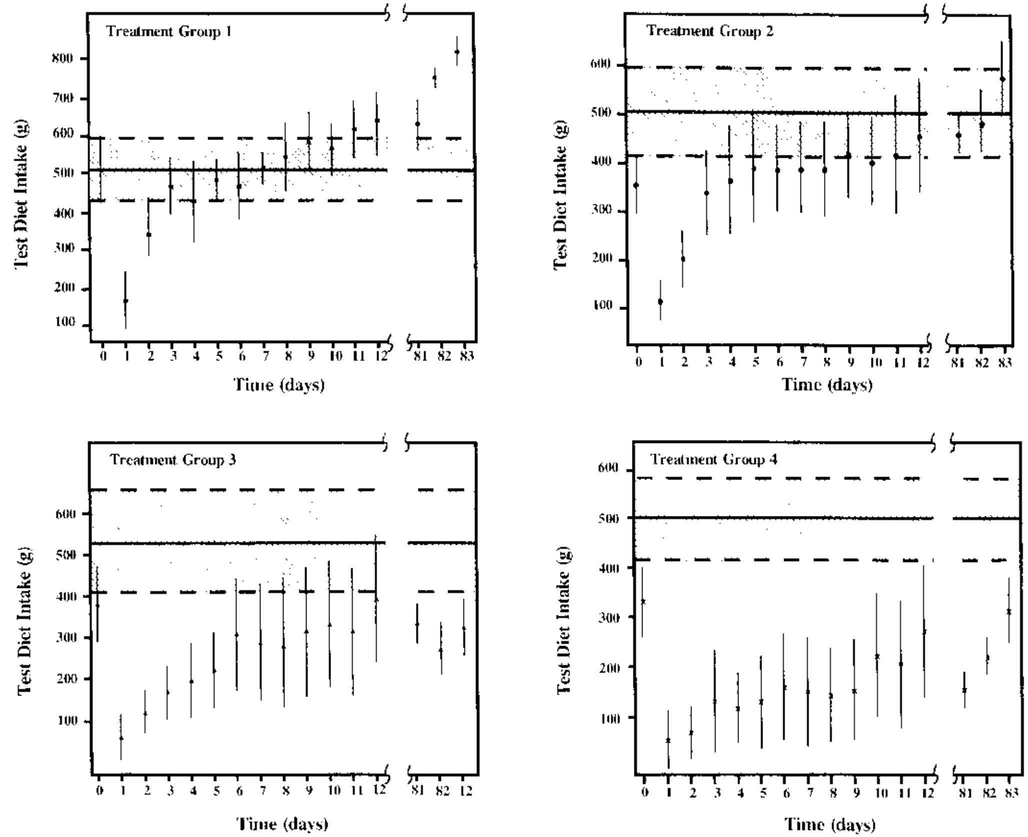


Fig. 1. Test diet intake by lambs (95% confidence interval indicated with bars) plotted against pre-exposure intake (95% confidence interval indicated with cross-hatched region). On day 0, lambs were offered foods for 1 h according to treatment design (Table 2) and immediately received lithium chloride (200 mg LiCl/kg body mass) by oral gavage. Lambs in treatment 1 had access to the test diet only; treatment 2 had access to test diet with 1% CA only. Lambs in treatments 3 (low energy alternative) and 4 (high energy alternative) had access to alternative food in addition to test diet with CA. (■)Treatment 1 (no choice: test diet); (●) treatment 2 (no choice: test diet (CA)); (▲) treatment 3 (two-choice: test diet (CA) and LEA); (★) treatment 4 (two-choice: test diet (CA) and HEA).

Inspection of the data demonstrated that extinction varied among treatments (Fig. 1). Based on the graphical data, extinction occurred on days 2, 3 and 6 for treatments 1, 2 and 3, respectively. Test diet intake in treatment 4 approached pre-exposure intake, but did not equal it at any point of the persistence trial as evidenced by the confidence intervals (Fig. 1). However, resumption of the bioassay following a 9-week intermission demonstrated that subjects in treatment 3 reduced intake to less than the pre-exposure level.

## 4. Discussion

This study was designed to evaluate the potential of FAL to reduce herbivory. Subjects were purposely familiarized with the test diet so that it would be representative of a familiar resource exploited by herbivores. A novel flavor (CA) was applied to the familiar test diet and lambs were averted to the flavored test diet. Following LiCl exposure, intake of test diet in the presence of novel flavor and alternatives was measured. Demonstrated preference of the test diet over the food alternatives was an important feature of this study.

Test diet intake was reduced in all treatments on day 1 as a result of lithium-induced aversion. To be useful as a management tool, FAL must result in significantly lower food intake versus pre-application intake. Furthermore, intake must be reduced for extended periods of time (i.e. the persistence of this aversion must be maximized). We defined extinction of the aversion as that day when post-exposure test diet intake was not significantly different from pre-exposure intake. This practical definition conforms to the anticipated application of FAL.

Extinction occurred rapidly in treatment 1, demonstrating the difficulty in forming aversions to familiar foods with a single UCS exposure. Latent inhibition contributed to the difficulty of forming an aversion due to the familiarity of the test diet (Schafe and Bernstein, 1996). CA was added to the test diet to change the flavor, thus increasing the likelihood of a persistent aversion. Subjects in treatment 2 avoided test diet with CA for a slightly greater duration than subjects offered test diet alone (treatment 1). However, the aversion was still short-lived because the subjects had no food alternatives. Given no choice, herbivores rapidly increase intake of a flavor paired with a toxin as they learn that the toxin is no longer present (Wang and Provenza, 1997).The inhibitory effects of CA on intake in the absence of an aversion also contributed to our results. In the bioassay which directly compared the effect of CA on intake of test diet, 1% CA reduced intake nearly 20% (745 g versus 597 g). Test diet intake on day 0 was similarly reduced versus pre-exposure intake in the main experiment when 1% CA was added to the test diet in treatments 2, 3 and 4 (Fig. 1). While these experiments did not fully resolve the two roles that CA played in limiting intake, data demonstrate that 1% CA both reduces intake in the absence of an aversion and is associated with lithium induced toxicosis.

In concert with the learned aversion, access to alternative foods reduced test diet intake more than addition of CA alone. The mere existence of the alternatives played a significant role in maintaining the aversion to CA-flavored test diet in treatments 3 and 4. Test diet intake in treatment 3 did not approach pre-exposure intake until day 6 of the experiment, while treatment 4 intake did not approach pre-exposure intake at any point of the experiment (Fig. 1). This is consistent with the theory that herbivores continuously sample small amounts of toxic foods as part of a long-term feeding strategy (Provenza, 1996). Given no choice, subjects in treatments 1 and 2 rapidly assessed that the test diet was not toxic.

In experiments such as this, lambs have been shown to prefer foods that best compliment the nutrient content of their basal ration (Wang and Provenza, 1996; Scott and Provenza, 2000). The basal ration in this study (alfalfa) was energy-deficient and protein-rich in comparison to the foods used in the experiment (Table 1). As a result, the nutritive value of the alternative food had a significant impact on persistence. Despite the fact that test diet was preferred over both alternatives in pre-exposure feeding trials, subjects relied on the alternatives to compliment the basal ration while attending to the aversion. However, subjects avoided CA-flavored test diet for a greater duration in treatment 4 versus treatment 3 because HEA better complimented the energy-poor basal ration versus LEA.

We measured test diet intake following a 68-day interruption of the experiment (Table 2). Spontaneous recovery of an aversion was reported in rats after an 18-day intermission but not after 49 days (Rosas and Bouton, 1996). Though extinction was demonstrated in treatments 1, 2 and 3 prior to intermission, test diet consumption by lambs in treatments 3 and 4 indicated avoidance of the CA-flavored test diet (Fig. 1). These data support previous evidence that prolonged avoidance of a cue in the absence of the UCS is possible (Kyriazakis et al., 1997). Spontaneous recovery would be a desirable feature of applied FAL because animals with previous exposure to a flavor paired with toxicosis would avoid that flavor without having to be re-conditioned.

In addition to demonstrating the importance of a salient cue, we found that both the presence of an alternative food and the nutritive value of the alternative played key roles in maintaining persistence. While avoidance was more persistent when the HEA was offered, even the presence of an LEA led to a significant reduction in test diet intake as compared to no alternative (Fig. 1). Our data suggest that the availability and nutritional characteristics of alternative forage are important to successful application of FAL to minimize herbivory.

Selection of an appropriate UCS (i.e. toxin) will be equally important to the success of applied FAL. While useful in experiments with captive species, LiCl does not hold any promise for use in applied FAL because it requires a large dose to produce an aversion (for example, 150–300 mg/kg in lambs). Future research in applied FAL must include identification of a suitable UCS for mammalian herbivores. Such a toxin should affect the emetic system (Garcia et al., 1985), produce aversions at low delivery concentrations, lack chronic or acute toxicity at delivery concentrations, be largely imperceptible to the herbivore (Conover, 1989) and have minimal persistence in the environment.

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